J. Physiol. (1969), **201**, *pp.* 1–19
With 10 *text-figures*
Printed in Great Britain

ELASTIC CONSTANTS OF THE HUMAN LENS CAPSULE

BY R. F. FISHER

From the Department of Physiological Optics, Institute of Ophthalmology, Judd Street, London, W.C. 1

(*Received* 18 *July* 1967)

SUMMARY

1. A technique is described whereby the elasticity of the human lens capsule has been determined at birth and throughout life. This technique requires three separate determinations: (*a*) thickness; (*b*) stress and strain; (*c*) Poisson's ratio; (*a*) the capsule was clamped between accurately perforated ground glass plates and its thickness determined by noting the change in depth of focus between Latex spherules adhering to its upper and lower surfaces; (*b*) the undisturbed capsule was then placed in a specially designed glass distension apparatus and the relationship between volume and pressure recorded when it was distended with isotonic saline. The permeability of the capsule was also measured; (*c*) in some cases Poisson's ratio was determined by measuring the change of thickness of the capsule and the height to which it rose when distended with isotonic saline at different pressures. An apparatus was designed for this purpose.

2. The average thickness of the anterior capsule increases from birth until about the 60th year but thereafter it decreases slightly.

3. Poisson's ratio was about 0·47 for both cat and human capsule, and no significant variations with age in human capsule could be detected.

4. Corrected volume pressure curves obeyed Hook's law almost to the point of capsule rupture.

5. In childhood Young's Modulus of elasticity is about 6×10^7 dyn/cm^2 and decreases to 3×10^7 dyn/cm^2 at 60 and $1{\cdot}5 \times 10^7$ dyn/cm^2 in extreme old age.

6. The ultimate tensile stress was $2{\cdot}3 \times 10^7$ dyn/cm^2 in young capsules and $0{\cdot}7 \times 10^7$ dyn/cm^2 in old ones. The maximum percentage elongation was 29 per cent and independent of age.

7. The implications of these findings are discussed in relation to

(*a*) the mechanical properties of the lens capsule;

(*b*) the ageing of the lens capsule and basement membranes; and

(*c*) the decrease in elasticity of the lens capsule as a cause of presbyopia.

INTRODUCTION

The elastic properties of the lens capsule were first demonstrated by Bowman (1849). He noted that a lens which had imbibed water and had become distended returned to its former shape when the lens capsule was punctured by means of a needle. The contained fluid was ejected with considerable force, demonstrating that the capsule was highly elastic. The extent of the elasticity of the capsule was questioned by Eisler (1930), who noted that when the capsule was torn, folds and wrinkles remained in the region of the tear. Fincham (1936) believed that the whole of the elastic properties of the lens resided in the capsule and the lens substance was plastic. Barraquer (1924) found that a 500 mg weight produced wide stretching of the equatoral region of the lens in an eye obtained from an 11-year-old child. Pau (1951) showed that the change in cylindrical dioptric power of the calf lens was proportional to the degree of stretching of the zonulo-lenticular complex. He found that a force of 1500 mg was required to produce a change of 2 dioptres. Adler (1959) noted that no quantitative measurements of capsular elasticity had ever been made, and Weale (1963) stated that the relative elastic contributions of capsule and lens substance in accommodation remained in the realm of speculation. This investigation was therefore undertaken to measure the elasticity of the lens capsule in absolute units. The variations in capsular elasticity, ultimate stress, and yield point throughout the life span were also studied and compared with those of elastic and collagenous tissue.

METHODS

Lens capsule preparation

Lenses were obtained from human cadavers not more than 48 hr after death. The capsule was cut around the equator of the lens with fine scissors and carefully separated from the lens substance with a small brush of marten's hair, while the lens was submerged in isotonic saline. The anterior part of the lens capsule was then examined under a phase contrast microscope to ensure that all trace of epithelium had been removed, and this portion of the capsule was used in all subsequent tests. It was important to discover if storage adversely affected the elastic properties of the capsule. Both lenses from the eyes of four cadavers were tested in pairs, the first eye on the same day and the second after storage at 4° C for a week. No significant differences in elasticity between the 2- and 9-day-old lenses was found. During this study human lens capsules were unobtainable for examination under 2 days old. Therefore post mortem changes in this period were not investigated. However, rabbit lens capsules when examined immediately or kept at room temperature for 2 days showed no appreciable difference in elasticity.

Young's Modulus of elasticity

The delicacy of the lens capsule necessitated the minimum of manipulation. This meant that it could be spread out on a glass plate only once since repeated spreading usually spoilt the preparation. The initial preparation was thus left undisturbed for subsequent

measurements and at all times kept bathed in isotonic saline. Initially the capsule was placed upon a circular optically flat glass disk carrying a central, accurately ground 4 mm perforation for thickness determination, and at a later stage the capsule was covered by another similar disk in order to measure its distensibility. This final preparation was then placed in a distension chamber and the capsule distended with isotonic saline, changes in pressure and volume being recorded by mercury manometer and a graduated glass capillary tube respectively.

1. *Measurement of average thickness of lens capsule*

The thickness of the lens capsule (t_m) was determined by covering its outer and inner surfaces with a suspension of latex spherules (0·8 μ diameter). The phase contrast microscope was then used to determine the thickness of the capsule to within 0·4 μ as follows:

The ground glass plate containing a drilled aperture was put on a special mount SF (Fig. 1*A*). This mount was designed to be flush with the ground glass surface of the plate GP. To examine the preparation the mount SF had to be removed, so a central hole AV was provided to allow access of air to the under surface of the lens capsule LM.

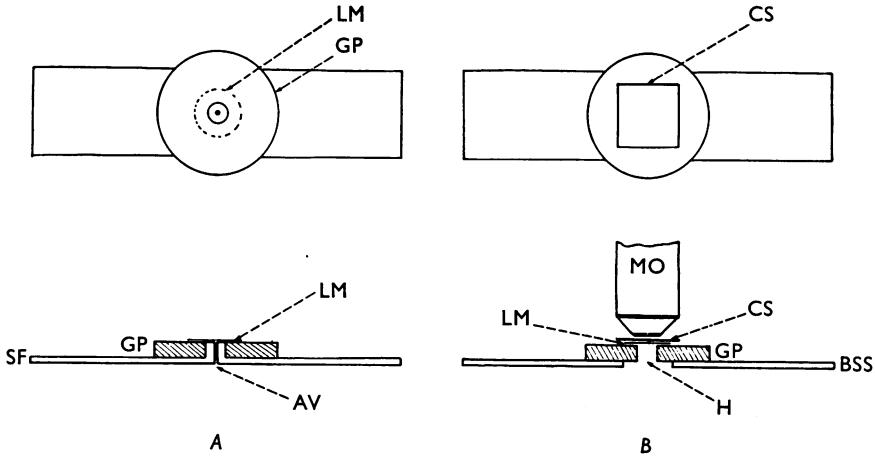

Fig. 1. Section and plan diagrams of apparatus for capsular thickness measurement.

A. The lens capsule LM is spread on combined flat surface of glass plate GP and brass mount SF fitted into plate perforation and flush with plate surface. Air vent AV facilitates removal of mount SF without capsule being disturbed.

B. Final mounting of preparation with glass plate GP resting on brass plate BSS for centring by mechanical stage of microscope. Microscope objective MO viewing lens capsule LM covered by cover-slip CS with mount SF removed. H, perforation (4·0 mm diam.) in ground glass plate.

Procedure. A drop of isotonic saline (NaCl, 0·9 g/100 ml.) mixed with a suspension of latex spherules was placed on the mount SF and glass plate. The capsule was then carefully spread over the hole in the glass plate. The upper surface of the capsule was then moistened with a further drop of saline and latex suspension and a cover-slip lightly placed in position. After the removal of the mount SF the glass plate was placed on a perforated brass stage plate BSS (2·5 × 7·5 cm). This enabled the preparation to be accurately centred by the mechanical stage of the microscope (Wild M-20) and viewed under the high power (Fig. 1*B*). Latex spherules adhering to the lens capsule could be identified since they were not undergoing Brownian movement. They were focused under phase contrast and the difference in focus

between spherules on the under surface and the upper surface of the capsule was determined. Three determinations of capsular thickness were made, at the centre of the lens capsule and at 1·5 mm on either side. The mean of these values was taken as the average apparent thickness of the capsule (capsular thickness equals 1·39 apparent thickness). To remove the cover-slip prior to clamping the glass plates in the pressure volume, or Poisson's ratio apparatus, the mount SF was replaced and the preparation immersed in a Petri dish filled with saline. The cover-slip could then be floated off without disturbing the capsule. A second perforated glass plate was then placed and centred over the first with the capsule held between them. After mount SF had been removed again the preparation was ready for the next measurement.

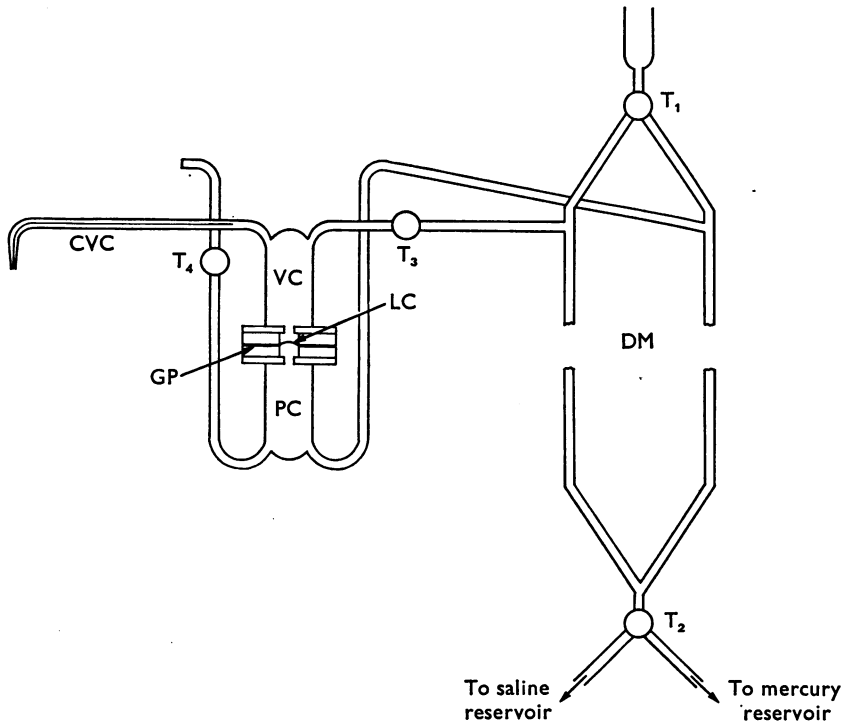

Fig. 2*A*. For legend see opposite page.

2. *Pressure volume measurement*

A glass apparatus (Figs. 2*A* and *B*) comprising two chambers blown from borosilicate glass and fitted with glass taps and joints ground to high vacuum tolerances was used. The upper chamber VC was connected to a graduated capillary tube CVC reading to 0·1 μl. and a lower pressure chamber PC. The two chambers could be bolted together after the glass plates containing the lens capsule had been placed between them, and were then sealed with silicone grease. A tap T_3 was employed to isolate the volume chamber from the differential manometer DM connected to both pressure and volume chambers. The tap T_4 was closed to the atmosphere when pressure was applied to the lower chamber. Before measured changes in volume and pressure could be related to the elasticity of the capsule, the initial volume and radius of the distended spherical segment of capsule had to be ascertained. The relationship between initial volume and radius of curvature of the spherical segment of capsule was

related to the dimensions of the perforation through which the capsule was distended, so that a measurement of the initial radius of the capsule in the apparatus was not required (Appendix eqns. (1–7) and (1–8); Figs. 9 and 10).

Procedure. The pressure chambers were separately filled with previously boiled and cooled isotonic saline in order to prevent the formation of air bubbles when the apparatus was warmed. The tap T_2 of the manometer DM was connected to the saline reservoir SR (Fig. 2*B*) and the manometer and connecting tubing filled with saline. After the pressure and volume chambers had been attached to the manometer they were placed in a water-bath

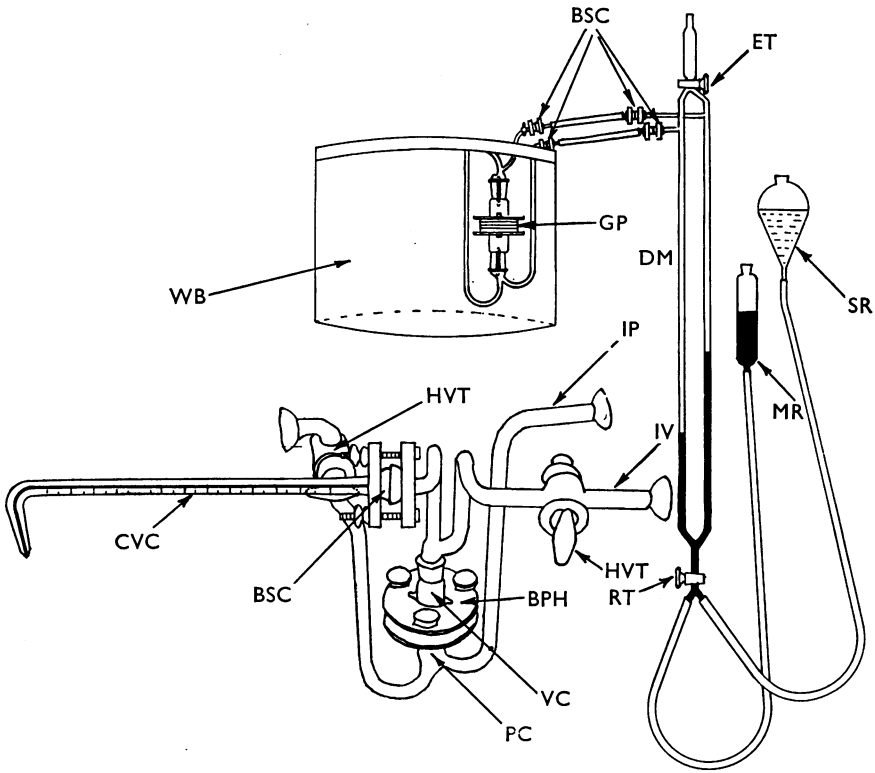

Fig. 2 *B*. Diagrams of apparatus for pressure, volume and permeability measurement.

A. Schematic view shows lens capsule LC lying between ground glass plates GP. The volume chamber VC and pressure chamber PC are connected to the differential monometer DM, changes being recorded by graduated capillary tube CVC. Tap T_2 successively connects saline and mercury reservoirs to manometer, while Tap T_1 equalizes pressure on either side of the membrane or separately connects limbs of manometer to the atmosphere. Tap T_3 isolates volume chamber from the manometer while Tap T_4 connects pressure chamber to the atmosphere.

B. General view shows whole assembly and isometric view of pressure volume apparatus. DM differential manometer, MR and SR mercury and saline reservoirs, ET and RT two-way taps above and below manometer. BSC glass joint connexions, WB water-bath (thermostat and stirrer not shown), BPH brass glass plate clamp. HVT high vacuum glass taps. IP and IV inlets to pressure and volume chambers.

maintained at 36·4 ± 0·05° C for 40 min (volume changes due to temperature fluctuations were not greater than 0·2 μl. after this time). The tap T_2 was next connected to the mercury reservoir and the tap T_1 across the limbs of the manometer. With volume and pressure chamber taps T_3 and T_4 open, mercury was run into the lower part of the manometer by raising the mercury reservoir. The pressure chamber tap T_4 was closed and fine adjustment of the volume of saline in the volume chamber was made by raising or lowering the mercury reservoir by means of a fine screw (not shown). By this method the saline meniscus in the capillary tube could be adjusted to zero. At this point pressure was the same on both sides of the capsule since manometer tap T_1 was connecting the upper and lower chambers of the apparatus. Tap T_3 was closed isolating the volume chamber from the manometer DM. The tap T_1 was then turned to connect the limb of the manometer previously connected to the volume chamber to the atmosphere. A slight fall (4 mm Hg) of the mercury level in this limb of the manometer was due to the saline in the manometer above the level in the rest of the apparatus. This was taken into account in subsequent pressure measurements. The mercury reservoir was raised to cause successive increases in pressure of about 20 mm Hg and corresponding volumes were read off on the graduated capillary tube. Readings were also obtained for decreasing pressure.

3. *Capsular porosity measurements*

As the dimensions of the membrane were small the volume changes were of the order of a few microlitres, and this necessitated the use of an incompressible fluid which did not influence the properties of the capsule. Although isotonic saline was ideal in these two respects, it had the disadvantage that its flow rate through the capsule had to be ascertained.

Procedure. The flow rate of the capsule was obtained by subjecting the capsule to a known pressure and measuring the increase in the volume of fluid in the volume chamber after 6 min. From these values a curve was constructed showing the variation with pressure (mm Hg) of capsular flow rate (μl./min) and it was found that this was proportional to pressure (Fig. 3, 2nd graph).

The values shown in this Figure are not absolute ones, but merely the flow rate in the entire membrane under test. This corresponds to a porosity constant of 130×10^{-8} cm/sec per cm head of water and being of the same order as mammalian glomerular basement membrane (300×10^{-8}–600×10^{-8}, Pappenheimer, 1953) suggests that the membrane was unlikely to be seriously damaged during preparation.

4. *Characteristics of pressure–volume curve*

After pressure had been equalized as described, successive increases of pressure were then applied to the capsule. In Fig. 3 (1st graph) the initial increase of pressure of 20 mm Hg produced a large change of volume (11 μl.) while smaller increments of pressure caused a non-linear increase in volume (not shown). This was due to the capsule *in vivo* conforming to the curved surface of the lens substance. Therefore it could not be completely flattened when placed between glass plates, and in consequence initial small changes of pressure caused large changes of volume. When completely distended to its former shape, however, pressure and volume showed a linear relationship when observed volumes were corrected for the permeability of the capsule (Fig. 3, 1st graph, continuous line). This correction for permeability could be ascertained if pressure readings were made at timed intervals. Half minute intervals were found suitable, and in order to continue the orderly sequence of readings, the final ascending pressure was also maintained for half a minute. When pressure was applied to the capsule an initial distension was obtained and recorded immediately. The volume of fluid continued to rise steadily in the graduated capillary tube due to flow of water through the capsule. Since a continuous series of increasing and decreasing pressures were applied to the capsule the increase in volume due to capsular permeability was cumulative (Fig. 3, dashed graph). As each pressure was applied to the capsule for a half minute

the corresponding volume of fluid which diffused through the capsule was calculated from its porosity curve. The sum of these volumes was then subtracted from the next observed volume caused by raising or lowering the pressure in the apparatus.

A corrected volume for the effect of pressure alone was thus obtained.

(*a*) *Initial volume.* The initial volume (v_0) was obtained from the corrected pressure volume curve (Fig. 3, 1st curve, continuous line) by extrapolation to zero pressure (in this case 11·4 μl.). At the beginning of the experiment at zero pressure the volume in the graduated capillary was adjusted to zero. Increases in pressure below 20 mm Hg caused large

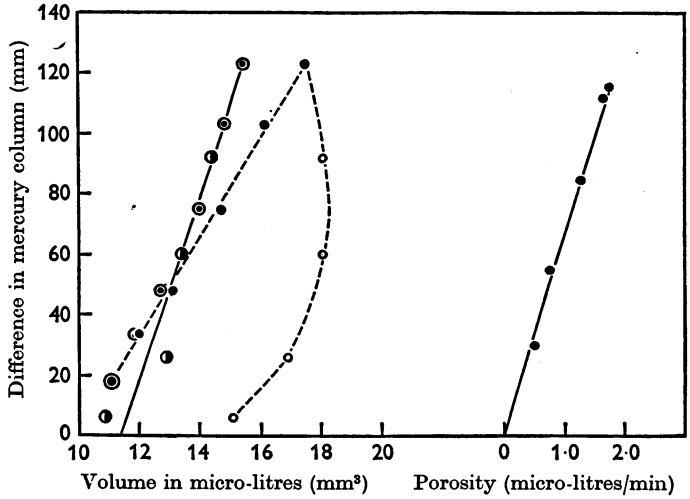

Fig. 3. Typical pressure–volume and porosity curves for a 45-year-old human lens capsule. Volume changes in microlitres plotted against pressure in mm Hg. Observed volumes recorded after corresponding pressure applied for half a minute. Porosity volumes in μl./min obtained by observing total volume change at a steady pressure for 6 min. Initial volume v_0 after porosity correction 11·4 μl. Change in pressure per unit volume $P/\delta v$ from gradient was 30 mm Hg/μl.

Observed volumes: increasing pressure ●---●; decreasing pressure ○---○. Corrected volumes: increasing pressure ⊙——⊙; decreasing pressure ◑——◑. $P' = 30$ mm/μl. $V = 11{\cdot}4$ μl.

increases in volume and the initial pressure (20 mm Hg) and the final pressure (5 mm Hg) gave similar volumes (11·0 μl.). As would be expected the incompletely flattened capsule had to be fully stretched to its curved lenticular shape before it resisted pressure changes to any great extent.

The initial volume was found to lie between 4 and 13 μl. with a reproducibility of $\pm 1{\cdot}5$ μl. From Fig. 10 this gives a value of VR of 16·0 mm^4 with a reproducibility $\pm 2{\cdot}0$ mm^4 at an initial volume of 6 μl. (an average value for the series).

(*b*) *Pressure per microlitre change in volume.* The pressure required to change the volume of the distended capsule by a microlitre (P') was obtained from the gradient of the corrected pressure volume curve (in this case 30·0 mm Hg/μl.). It was noted that when the capsule was fully stretched about 15 times the pressure was required to change the volume by a microlitre. The reproducibility of this pressure (P') on the same capsule was $\pm 2{\cdot}0$ mm Hg when the pressure was about 25 mm Hg per microlitre. Three pressure–volume curves were obtained from each capsule. The values for initial volume (v_0) and change in pressure per

microlitre change in volume (P) were measured and then averaged after each curve had been corrected for capsular permeability.

5. *The calculation of Young's Modulus of elasticity*

Figure 4 illustrates, in a specimen chosen at random, the relationship between the corrected pressure-volume curve A, and the calculated stresses and linear strains curve B, produced in the lens capsule. The values of stress and strain in the derived curve B were calculated from the equations in Appendix 1. An estimate of the initial arc length of the specimen (l_0) was the average of distances measured on projections of seven lens photographs.

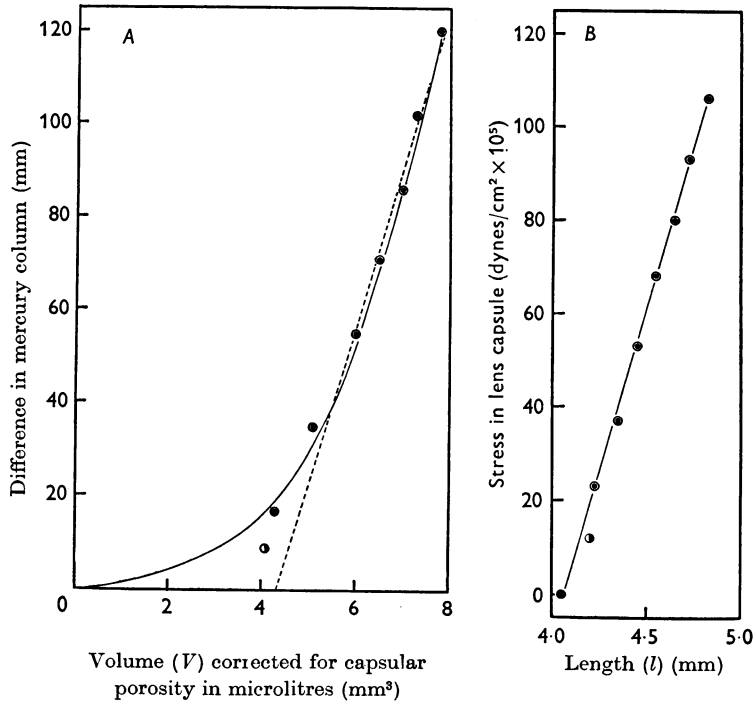

Fig. 4. A. Corrected pressure volume curve for a 30-year-old lens capsule. ⊙—⊙ increasing pressure; ◑ decreasing pressure; - - - straight line fitted to linear portion of curve. B. Corresponding arc length of capsule (mm) and calculated stress (dyn/cm²) for each point on curve A, with the exception of original length (filled circle). Original length measured from lens profile photographs (see text).

The method of photographing the lens is described in the subsequent paper. The arc length was measured along the curved lens profile by means of a wheel rule, and was obtained as follows. First, a line was drawn on the traced profile parallel to the lens equator and so adjusted that the distance along this line between the two sides of the profile margins represented the diameter of the glass plate perforation (4 mm). Secondly, the curved length of the lens profile was measured between the points of intersection of the lens outline and this parallel line. This initial capsular length could only be presumed to equal the amount of capsule eventually clamped between the glass plates.

However, when the value of capsular stress is reduced to zero (Fig. 4 B) good agreement is obtained between the arc length of the capsule on the lens and that between the glass

plates (Fig. 4*B*) (filled circle). Furthermore, despite the cumulative correction for permeability when the pressure is reduced to 8·0 mm mercury the residual extension (half filled circle) was only 0·1 mm greater than expected. The extension of the capsule within this stress range therefore was truly elastic, and no appreciable slippage of the specimen between the glass plates can have occurred.

Figure 5 shows the theoretical relationships between linear and volume strains. It will be seen that for volumes greater than 8·0 μl. linear strain is almost exactly one third volume

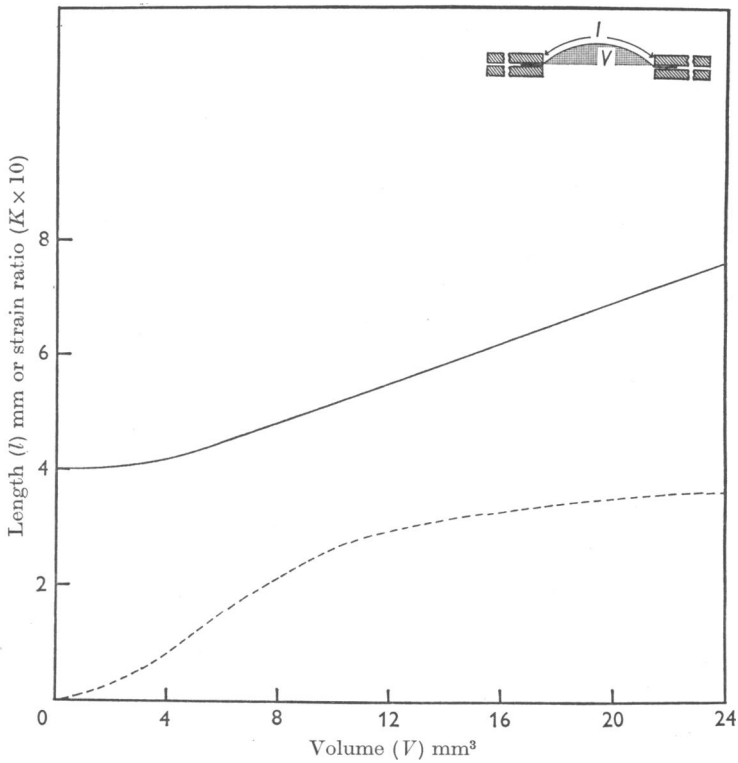

Fig. 5. Theoretical relationship between volume of distended spherical capsular segment volume (V) plotted, first, against arc length of specimen (l; continuous curve) and, secondly, against ratio of linear strain to volume strain (K; dashed curve). K = linear strain/volume strain.

strain. This clearly justifies the calculation of Young's Modulus directly from volume changes, without a series of derived stress strain graphs being plotted.

Young's Modulus was calculated therefore from Appendix Eqn. 1.18

$$E = \frac{3}{2} \cdot \frac{P'R}{t_m} \cdot (1-\sigma) \cdot v_0$$

where E = Young's Modulus of elasticity,
t_m = average thickness of lens capsule,
R = radius of curvature of the capsule in the apparatus,
v_0 = the initial volume of the capsule in the apparatus,
P' = change in pressure mm Hg per microlitre change in volume,
σ = Poisson's ratio.

For the capsule shown in Fig. 4, $E = 5{\cdot}2 \times 10^7$ dyn/cm^2 calculated from volume strains (Fig. 4*A*). Young's Modulus differs by only $0{\cdot}1 \times 10^7$ dyn/cm^2 from this value when calculated from linear strains (Fig. 4*B*).

It has been noted that the capsule under low pressure rapidly assumes a radius of curvature of about 2·0 mm. This might be thought to be due to non-elastic or unequal stretching. Figures 5 and 10 show that a more probable explanation is that initially large changes of radius of curvature occur with small changes of linear or volume strain. If, for example, it be assumed that the anterior polar radius of curvature of the lens is 6·0 mm (Fincham, 1936), then the entire volume of the anterior segment would be 2·5 μl. (Fig. 10). This would correspond to an arc length of 4·05 mm (Fig. 5). Doubling the volume of the capsular segment in the apparatus (5·0 μl.) would only require an increase of arc length of 0·05 mm (Fig. 5) but the radius of curvature would be reduced to 2·5 mm (Fig. 10).

A change in radius of curvature therefore of over 200 % is produced by a linear strain of about 1 %. Thus the capsule under pressure rapidly assumes a hemispherical shape and failure has been repeatedly observed to occur as would be expected along a diametral plane, i.e. at or near the edge of the glass plate perforation.

6. *Poisson's ratio measurements*

This required the measurement of the area and thickness of the capsule when partly and fully distended. The initial and final pressures stretched the capsule and caused it to form a spherical surface in the hole of the glass plate. The height to which this surface rose could be related to the change in surface area of the capsule while the change in thickness was measured directly by the method described in the first section. Determinations were made for six human, two rabbit and two cat capsules but it was found that more reliable results could be obtained from the cat capsule as it was about 6 times as thick as human capsule.

The apparatus (Fig. 6) comprised a pair of clamped and perforated glass plates GP. The capsule LM was placed between them and they were attached to a pressure chamber PC and mounted on the mechanical stage of the microscope. The pressure chamber was connected to a saline reservoir which could be raised above the preparation. Some air was left in the pressure chamber as this prevented the latex spherules being forced off the capsule by diffusing saline.

Procedure. After the capsule was clampled between the glass plates it was distended with saline at low pressure (5 cm H_2O); the low power objective of the microscope was focused in turn on the apex of the upper surface of the capsule and the upper surface of the glass plate, the heights of the objective being successively recorded. The thickness of the upper glass plate was added to this measurement to obtain the true height to which the capsule was distended. The apical thickness of the capsule was then measured as described previously. Depending on its thickness a high or low power objective was used. These measurements were again repeated at a higher pressure (30 cm H_2O). Finally, measurements were again taken at the initial low pressure to confirm that the capsule returned to its original distension and thickness. It follows that the measurements were made within the range of strain reversibility. Poisson's ratio was calculated from Appendix Eqn. 2.4)

$\sigma = 2st(r^2+h_1^2)/t.(h_2^2-h_1^2)$, where

σ = Poisson's ratio,

st = change in capsular thickness (about 10–20 μ for the cat),

h_1, h_2 = initial (1·0–1·5 mm) and final (1·75–2·25 mm) apical height of capsule,

r = radius of glass plate perforation (2·0 mm),

t = apical thickness of capsule (65–75 μ for the cat).

RESULTS

Thickness of the anterior part of the capsule. Salzmann (1912) showed that there was a gradual increase in the thickness of the anterior part of the lens capsule until about the 6th decade and thereafter a slight decrease. To compare these figures with the present results, average values of capsular thickness of neonatal capsules, capsules per decade from 10 to 70 years, and capsules over the age of 75 years were plotted with Salzmann's values in Fig. 7. Salzmann's values included estimations of capsular thick-

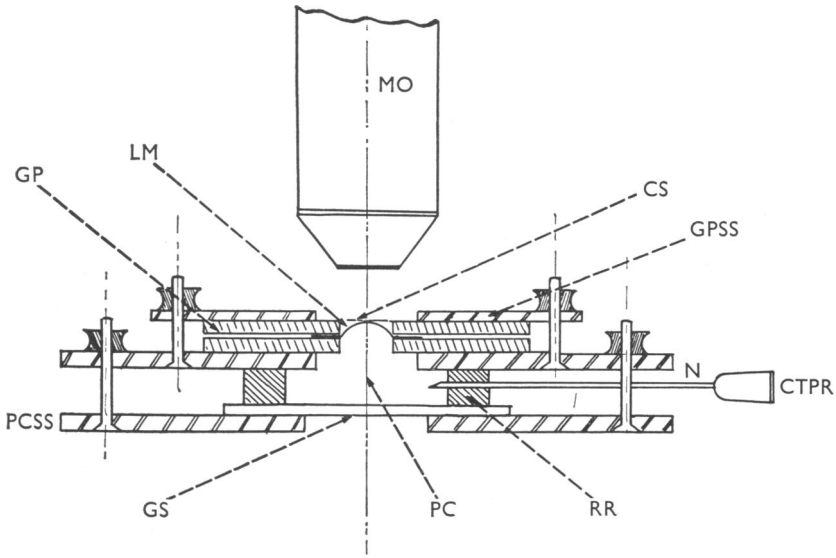

Fig. 6. Sectional diagram of apparatus for Poisson's ratio measurement. The lens capsule LM is clamped between glass plates GP held in position by glass plate separate section clamp GPSS. The pressure chamber PC comprising rubber ring RR, glass slide GS and hypodermic needle N is assembled and clamped by pressure chamber separate section clamp PCSS. A portion of cover slip (2·0 mm × 2·0 mm) CS is placed on saline covered capsule and the preparation observed by microscope objective MO, when whole assembly is placed on mechanical stage of microscope. Connector CTPR is connected to saline reservoir (not shown) by plastic tubing.

ness nearer the equator of the lens but the mean values of both series showed similar increase throughout the greater part of life with a slight decline in old age.

Pressure–volume relationships. Figures 3 and 4*A* show the pressure–volume curve of a 45- and 30-year-old lens capsule. The corrected pressure–volume curve was almost a straight line between 50 and 120 mm Hg. At higher pressures the capsule was stressed above its elastic limits. In this region volume changes increased disproportionately but usually the capsule ruptured suddenly without much further increase in volume.

Poisson's ratio. The human lens capsule showed a change in thickness of only 2–4 microns when Poisson's ratio was determined by the method described. With such a small change the error of this method is great ($\pm 25\%$) and in consequence it was not possible to determine whether there was a senile change. The cat capsule, however, being so much thicker showed a change in thickness between 10 and 20 μ and the error, although the low power objective had to be used, was correspondingly less ($\pm 15\%$).

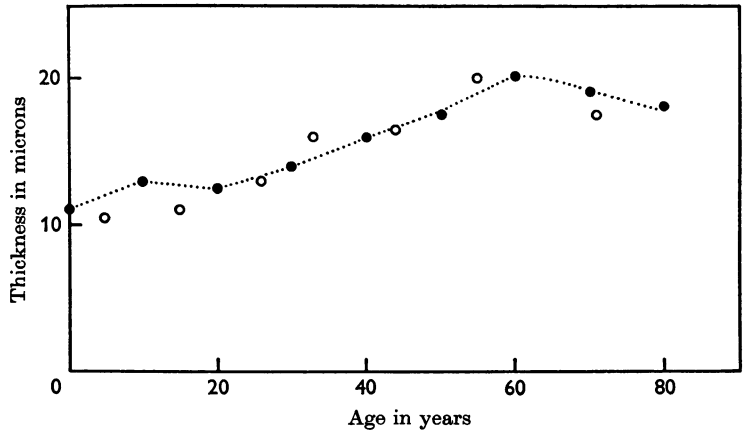

Fig. 7. Average thickness of anterior lens capsule in microns plotted against age. Initial plotted point mean value of capsule up to the age of 1; final plotted point mean value of capsules above age of 75. Intermediate plotted points mean value of capsular thickness per decade. Present data are average of thickness of centre of capsule and 1·5 mm on either side. ● Present data; ○ Salzmann's data.

The average value for ten determinations was 0·47 (S.D. $\pm$ 0·05): (six human, two rabbit, two cat capsules) and no difference was detected between these species. Since the loose texture of the capsule has been revealed by electronmicroscopy, it could be argued that fluid would be squeezed out of the capsular interstices when pressure was applied to it.

The behaviour of the capsule under stress, if not strained beyond the elastic limits, does not support this view, since on reducing pressure it returns to its previous thickness. A more cogent fact was the value obtained for Poisson's ratio. As this was almost constantly 0·5 it showed that practically no change in volume occurred, so in this respect the capsule had very similar properties to rubber. If fluid had been squeezed out of a capsule with a sponge like structure, the volume would have decreased markedly under pressure causing Poisson's ratio to be above its known range of 0·25–0·5 for most elastic substances. Then the capsule could not have been treated as a homogeneous rubber-like substance for the purpose of calculating Young's Modulus of elasticity. Furthermore, since

in both these determinations the capsule is stretched by internal pressure in the same way as when *in situ* on the living lens, the value of Poisson's ratio is of particular relevance.

Young's Modulus of elasticity. In Fig. 8 the value of Young's modulus is plotted against age for thirty human lens capsules. The elasticity ranges from about 6×10^7 dyn/cm^2 in infancy to 2×10^7 dyn/cm^2 in old age. Throughout life Young's Modulus steadily decreases, but the rate of decrease at different ages slightly varies. Young's Modulus of elasticity shows a very significant correlation with age ($r - 0{\cdot}82$, $P < 0{\cdot}001$).

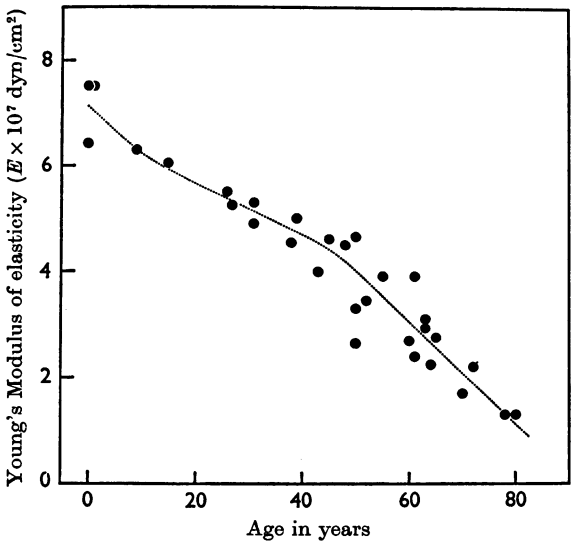

Fig. 8. Young's Modulus of elasticity plotted against age for the anterior part of thirty human lens capsules, each point being the mean value of three determinations per capsule. Central portion of capsule tested (4·0 mm diameter) with a thickness (t_m) variation between 9 and 22 μ, and pressure of distension between 0-120 mm Hg recorded volume changes corrected for capsular porosity. In calculating Young's Modulus a value of 0·47 for Poisson's ratio was used.

Ultimate stress. The maximum stress which the human capsule could sustain before sudden rupture was about $2{\cdot}3 \times 10^7$ dyn/cm^2 in capsules below the age of 20 and $0{\cdot}7 \times 10^7$ dyn/cm^2 in those above 70 years.

Percentage elongation. As the human lens capsule tears so easily when stretched in one direction it was not possible to measure the percentage elongation by simple extension. The maximum percentage linear elongation of the human capsule which occurred before rupture was therefore calculated from the volume relationship. Appendix eqn. (1.15). It amounted to 29 % irrespective of age.

DISCUSSION

Elastic constants of the lens capsule. A summary of the properties of human lens capsule, rat collagen and human aortic tissue is shown in Table 1. Such a table shows these properties numerically, but a comparison between them is more easily appreciated by imagining that the human lens is surrounded in turn by tissue of the same thickness as its own capsule but with the properties of collagen and elastic tissue.

When accommodation relaxes, the equatorial diameter of the human lens increases by as much as 1 mm (Fincham, 1937). If the average diameter of the lens is taken as 9 mm this increase corresponds approximately to an area change of 13%. Since area strain is twice longitudinal strain this corresponds to a percentage elongation of 6·5%. Human lens substance

TABLE 1

Tissue	Young's Modulus of elasticity (dyn/cm²)	Maximum % elongation
Lens capsule (human)	$2{\cdot}0$–$6{\cdot}0 \times 10^7$	29
Collagen (rat) (Verzar, 1964)	300×10^7	5
Aortic elastic tissue (human)	$0{\cdot}3 \times 10^7$ (Burton, 1954)	127 (Ayer, Hass & Philpott, 1958)

surrounded by a collagenous capsule could at one stage be subject to a force 66 times greater than is true for its natural capsule. The collagenous capsule would, however, rupture if the lens changed to the unaccommodated state, since the limit of elongation would have been passed by at least 1·5%. Similarly, an imaginary human lens capsule of human aortic tissue could be extended 9 times further before it ruptured, when the lens changed from the accommodated to the unaccommodated state. However, the force transmitted to the lens substance would only be one thirteenth of the force actually exerted by the natural human lens capsule. This concept illustrates the fact that the human lens capsule has properties intermediate between collagen and elastic tissue, which produces an effective compromise between excessive lens moulding pressure associated with small elongation, and insufficient force coupled with great elongation.

Lens capsule and other basement membranes. The decrease in Young's Modulus of elasticity which occurs with age in human lens capsules may be of wide significance since the lens capsule is probably a re-duplicated basement membrane. The fluorescent antibody technique has provided evidence for this idea as the capsule possesses antigens similar to those of the basement membrane of small blood vessels and kidney glomeruli (Krakower & Greenspan, 1964; Roberts, 1957). Basement membranes throughout an individual's body may therefore be influenced by age in a fashion similar to that observed for the lens capsule.

Capsular elasticity and ageing. By the age of 60, Young's Modulus of elasticity has fallen to about one half the value in infancy. Saxton (1942) found that the tensile stress of human elastica decreased with age, while Kirk & Chieffi (1962) showed that the elastic recoil of the skin, especially in those regions exposed to daylight decreased with age. The changes in the human lens capsule with age are therefore similar to those observed in other elastic tissue.

Vogt (1930) was the first to propose that loss of accommodation could be caused by a loss of elasticity of the lens capsule. The present data show that the force which could be transmitted to the lens substance per unit thickness of lens capsule falls to about one half by the age of 60. However, the force which can be transmitted to the lens also depends on the thickness of the capsule and this increases until the age of 60, so that there is some compensation for the loss in elasticity. The only reliable method of assessing the effect of capsular changes upon accommodation is to calculate the amount of stored energy in the capsule which is released during accommodation. This is the subject of the subsequent paper.

I would like to acknowledge the encouragement given to me by Dr R. A. Weale, and the technical assistance of Miss B. Scott.

APPENDIX

1. *Young's Modulus of elasticity*

Figures 4, 9 *and* 10. When anterior lens capsule is in distension apparatus, let

l = arc length of capsular segment (mm),
v_0 = initial volume of capsular segment (mm^3),
2α = angle subtended by the capsular segment at its centre of curvature,
R = radius of curvature of capsular segment (mm),
h = height of apex of capsular segment (mm),
t_m = mean thickness of capsule (μ) ($mm \times 10^{-3}$),
P = internal pressure (mm Hg),
f = tangential stress in capsule (dyn/cm^2),
e_c = circumferential strain caused by internal pressure (i.e. $\delta l/l$),
V = volume of capsular segment (mm^3),
A = area of capsular segment (mm^2),
σ = Poisson's Ratio,
E = Young's Modulus of elasticity (dyn/cm^2).

(*a*) *Stress in capsular segment.* Force tending to cause failure at AB marking out a thin ring of capsule

$$2\pi R \cos\theta R\,\delta\theta\,.P \qquad (1.1)$$

Vertical component of this force

$$2\pi R^2 \sin\theta \cos\theta \, \delta\theta P. \tag{1.2}$$

Total force tending to cause failure at margin of hole in glass plate

$$= \pi R^2 P \int_{(\frac{1}{2}\pi-\alpha)}^{\frac{1}{2}\pi} \sin 2\theta \, \mathrm{d}\theta = \pi . R^2 P \sin^2\alpha. \tag{1.3}$$

Total force at margin of membrane

$$= 2\pi R t_m \cos(\tfrac{1}{2}\pi - \alpha) f = 2\pi R t_m \sin\alpha f.$$

Vertical component of this force

$$= 2\pi R t_m \sin\alpha \sin\alpha f = 2\pi R t_m \sin^2\alpha f \tag{1.4}$$

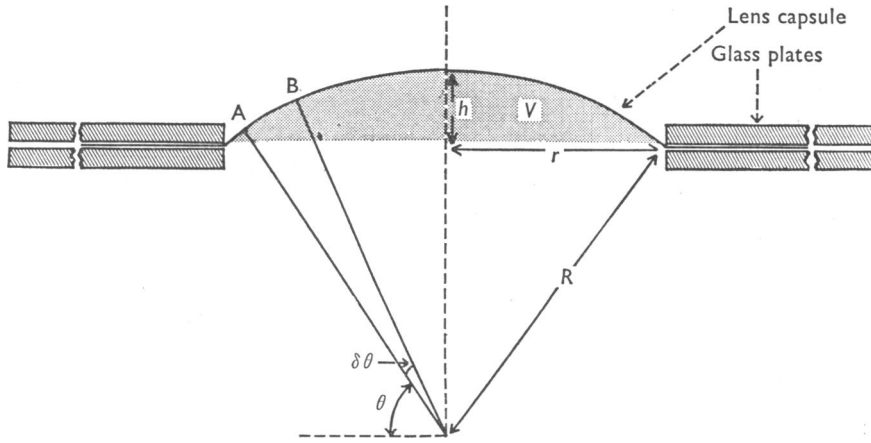

Fig. 9. Diagram of distended capsule in pressure-volume apparatus. Shaded area represents volume of fluid contained in the segment of a sphere enclosed by the capsule. Radius of plate perforation r (2·0 mm). Variable radius of curvature of capsule R and variable height of segment h depending on degree of distension of capsule in apparatus. AB small ring of capsule subtending in angle $\delta\theta$.

Stress in segment as for whole sphere

$$= f = RP/2t_m. \tag{1.5}$$

(*b*) *Circumferential strain in capsular segment.* The circumferential strain e_c is due to two principal stresses acting at right angles (radial stress is neglected since the capsule is thin), then

$$e_c = f/E - \sigma f/E. \tag{1.6}$$

The first term in (1.6) is due to principal stress acting along the circumference and the second term is due to an equal stress acting at right angles to the first principal stress. This circumferential strain may be determined

from the arc length (l) and the change in surface area of the capsular segment (SA) as follows. From the geometric properties of the segment (Fig. 9)

$$R = (h^2+r^2)/2h, \tag{1.7}$$

$$V = \tfrac{1}{3}\pi.h^2(3R-h), \tag{1.8}$$

$$\alpha = \sin^{-1}r/R = \sin^{-1}[2hr/(h^2+r^2)], \tag{1.9}$$

$$l = 2\alpha R = \alpha(h^2+r^2)/h. \tag{1.10}$$

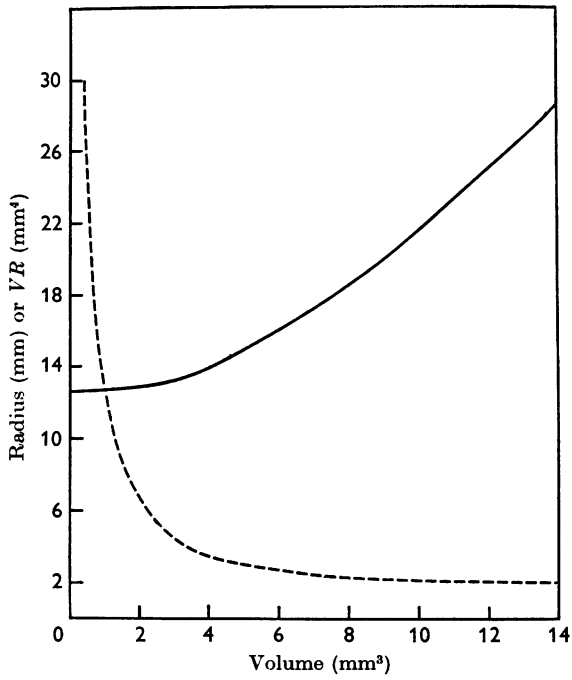

Fig. 10. Theoretical relationship between volume of (4·0 mm diameter) distended spherical capsular segment V plotted, first, against capsular radius of curvature R (dashed line) and, secondly, against the product of segment volume and radius of curvature VR (continuous line). Note that when capsular segment volume is greater than 8·0 μl. the capsular radius of curvature in the apparatus is almost constant at 2·0 mm.

Area of capsular segment

$$A = 2\pi Rh = \pi(h^2+r^2). \tag{1.11}$$

Volume of capsular segment

$$V = \tfrac{1}{6}\pi(h^3+3h^2r) \tag{1.12}$$

(from eqns. (1.7) and (1.8)).

Differentiating (d/dh) eqns. (1.11) and (1.12) and combining to exclude dh

$$\mathrm{d}A/A = \tfrac{2}{3}[h^2(h^2+3r^2)/(h^2+r^2)^2]\,\mathrm{d}V/V. \tag{1.13}$$

A first-order approximation gives area strain as twice the linear strain since the stress at all points of the segment is the same (eqn. 1.5).

$$e_c = \tfrac{1}{3}[h^2(h^2+3r^2)/(h^2+r^2)]\,\mathrm{d}V/V. \tag{1.14}$$

For a 2·0 mm perforation

$$e_c = \tfrac{1}{3}[h^2(h^2+12)/(h^2+4)^2 \quad \text{volume strain.} \tag{1.15}$$

If K = linear strain/volume strain then

$$K = \tfrac{1}{3}[h^2(h^2+12)/(h^2+4)^2]. \tag{1.16}$$

(c) *Volume strain in capsular segment.* For volumes greater than 8·0 μ (Fig. 5)

$$K \simeq \tfrac{1}{3}.$$

From eqns. (1.6) and (1.5).

$$\text{Circumferential strain} = \frac{PR}{2t_m E}(1-\sigma) \tag{1.17}$$

and since $K = \frac{1}{3}$ from eqn. (1.15).

$$E = \frac{3}{2}\frac{PR}{t_m}(1-\sigma)\frac{v_0}{\delta v}$$

$$= \frac{3}{2}\frac{P'R}{t_m}(1-\sigma)\,v_0 \quad (\text{where } P' = P/\delta V). \tag{1.18}$$

In the differential water mercury manometer 1 mm Hg = 12·34 dyn/mm^2 and δV = 1·0 mm^3

$$\text{Then } E = 0{\cdot}982\,P.Rv_0/t_m \times 10^6 \text{ dyn/cm}^2. \tag{1.19}$$

Note: Rv_0 is obtained from Fig. 10.

2. *Poisson's ratio*

For the Poisson's ratio apparatus let

A_i = initial area of surface of capsule,
A_f = final area of surface of capsule,
h_1, h_2 = initial and final height of capsule,
t = the apical thickness of capsule,
δt = change in apical thickness of capsule,
r = radius of glass plate perforation,
R = radius of curvature of capsule,
σ = Poisson's ratio.

Final area of segment from eqn. (1.11)

$$= A_f = \pi(h_2^2+r^2). \tag{2.1}$$

Initial area of segment

$$= A_i = \pi(h_1^2+r^2). \tag{2.2}$$

Area strain

$$= \frac{A_f-A_i}{A_i} = (h_2^2-h_1^2)/(h_1^2+r^2). \tag{2.3}$$

σ = lateral strain/$\frac{1}{2}$ area strain

$$= (\delta t/t)/\tfrac{1}{2}(h_2^2-h_1)/(h_1^2+r^2)$$

$$= 2.\delta t.(h_1^2+r^2)/t(h_2^2-h_1^2). \tag{2.4}$$

REFERENCES

ADLER, F. H. (1959). In *Physiology of the Eye*, p. 248. St Louis: C. V. Mosby Co.

AYER, J. P., HASS, G. M. & PHILPOTT, A. (1958). Aortic elastic tissue. *Archs Path.* **65**, 519–544.

BARRAQUER, I. (1924). *Cataracta Senil Metodos Operatorios.* Barcelona: W. A. Fisher, Claraso.

BOWMAN, W. (1849). *Lectures on the Parts Concerned in the Operations on the Eye and on the Structure of the Retina.* London: Longmans.

BURTON, A. C. (1954). Relation of structure to function of the tissues of the wall of blood vessels. *Physiol. Rev.* **34**, 619.

EISLER, P. (1930). Descemetsche Haut und Linsenkapsel. *Albrecht v. Graefes Arch. Ophthal.* **124**, 705–707.

FINCHAM, E. F. (1936). Experiment on influence of tension upon form of crystalline lens. *Trans. ophthal. Soc. U.K.* **56**, 138–147.

FINCHAM, E. F. (1937). The mechanism of accommodation. *Br. J. Ophthal.* **21** (Monograph Supplement VIII).

KIRK, J. E. & CHIEFFI, M. (1962). Variation with age in elasticity of skin and subcutaneous tissue in human individuals. *J. Geront.* **17**, 373.

KRAKOWER, C. A. & GREENSPAN, S. A. (1964). In *Diabetes Mellitus*, p. 161. Washington: American Institute of Biological Science.

PAPPENHEIMER, J. R. (1953). Passage of molecules through capillary walls. *Physiol. Rev.* **33**, 387–423.

PAU, H. (1951). Zur Mechanik der Akkomodativen Linsenverschiebung. *Albrecht v. Graefes Arch. Ophthal.* **151**, 565–573.

ROBERTS, D. ST C. (1957). Studies on the antigenic structure of the eye using the fluorescent antibody technique. *Br. J. Ophthal.* **41**, 338.

SALZMANN, M. (1912). In *The Anatomy and Biology of the Human Eyeball in the Normal State*, p. 165. Chicago: University of Chicago Press.

SAXTON, J. A. (1942). Decrease in tensile strength of elastic tissue. *Archs Path.* **34**, 362.

VERZAR, F. (1964). In *Aging of the Collagen Fibre*, International Review of Connective Tissue Research, vol. 2. New York and London: Academic Press.

VOGT, A. (1930). *Lehrbuch und Atlas der Spaltlampenmikroskopie des lebenden Auges*, vol. 1. Berlin: J. Springer.

WEALE, R. A. (1963). In *The Aging Eye*, p. 85. London: H. K. Lewis & Co. Ltd.